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SEASONAL POND CHARACTERISTICS ACROSS A CHRONOSEQUENCE OF ADJACENT FOREST AGES IN NORTHERN MINNESOTA, USA

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Abstract: Small seasonal ponds are abundant in many forest landscapes, yet they remain poorly understood in terms of their response to disturbance of the surrounding upland forest. The potential for such a response is large because of the small size and, hence, high perimeter-to-area ratios of most ponds. High perimeter-to-area ratio may increase the importance of functional connections with the surrounding forest, via exchange of energy, organisms, and materials. To better understand this connection, we studied 19 seasonal ponds across a 100-year chronosequence of single-cohort forests in northern Minnesota. Our objective was to see if there are distinct changes over time in select pond attributes, which may reflect alteration of functional linkages with the surrounding forest. In 1998 and 1999, we sampled hydroperiod, water depth and chemistry, canopy openness, grass, sedge, shrub, and coarse woody debris cover, coarse particulate organic matter (CPOM) flux, and macroinvertebrate and amphibian populations. We related these variables to stand age through regression. Stand age explained little variation for most variables. Responsive variables included canopy openness and CPOM flux. Canopy openness, in turn, was related positively to total macroinvertebrate abundance, sensitive taxon richness, and Haliplidae beetle and Physidae snail abundances. Calling wood frogs occurred more frequently under an open canopy and low CPOM flux. An open canopy, which occurs more often over ponds in younger than in older forest, likely results in increases in water and air temperatures and photosynthetically active radiation, all of which may influence resource availability and habitat suitability for some macroinvertebrates and amphibian taxa. Results from our exploratory study suggest that many characteristics of small seasonal ponds are unaffected by harvest of the adjacent upland forest, at least as detected through examination of a chronosequence. However, responsive variables may include several abiotic characteristics that provide mechanistic links to pond foodwebs

Key Words: seasonal forest ponds, forest disturbance, wetland invertebrates, amphibians, forest-pond interactions

INTRODUCTION

Small seasonal ponds are abundant in many forested landscapes of North America, yet they remain one of our more poorly understood ecosystems. Seasonal ponds are unique because of their hydroperiod, which often includes a dry phase, but also because of their size, which is generally much less than 1 ha (e.g., Brooks et al. 1998). Small size results in high perimeter-to-area ratios, which may increase interaction with the adjacent forest via exchange of energy, organisms, and materials. Consequently, one can predict that disturbances in the adjacent forest may affect composition of biotic communities and trophic structure of pond ecosystems through changes in insolation, organic matter input, water chemistry, and hydrology.

Removal of the forest surrounding seasonal ponds should increase light availability, due to reduced canopy cover, and decrease coarse particulate organic matter influx, similar to the effects of forest removal adjacent to small streams (Webster et al., 1990, Brosofske et al. 1997). These changes, in turn, could cause important changes in invertebrate communities and trophic structure, as has been shown for headwater streams (Wallace et al. 1997). The distinction between small seasonal ponds and small streams is that ponds often support a plant community within their basins (e.g., Batzer et al. 2000), providing an autochthonous source of shade and detritus. Thus, the strength of the functional linkage between the pond system and the adjacent upland forest, and the extent that disturbance of the surrounding forest alters pond attributes, may not be as important as it is for headwater streams.

We have only limited empirical data on the influence of adjacent forest disturbance on seasonal pond characteristics. In a recent retrospective study from southern pine plantations, Batzer et al. (2000) found a variety of stand age-related patterns in seasonal pond characteristics, including negative correlations between stand age and light availability, water temperature, sedge biomass, cladoceran numbers, and terrestrial invertebrate richness and positive correlations between age and maximum water depth, electrical conductivity, and aquatic oligochaete numbers. Pond pH showed a strong curvilinear relationship with age, peaking in 10- to12-year-old stands. A number of pond characteristics showed no relationship with stand age, including hydroperiod, dissolved oxygen levels, sediment input, macrophyte diversity, periphyton biomass, and density of most aquatic invertebrates. A drawback of that study was the short length of the chronosequence (23 years), which reflects the commercial rotation age for plantations in the region.

To understand the importance of linkages between seasonal ponds and adjacent upland forest better, we examined relationships between a number of pond attributes and age of surrounding forest using 19 seasonal ponds spanning a 100-year chronosequence of aspen (*Populus* spp.)-dominated ecosystems in northern Minnesota. Specifically, we asked if there are identifiable changes in abiotic and biotic pond variables across the stand-age sequence that may relate to post-harvest changes in forest structure.

As with any chronosequence, we assumed that the study ponds and surrounding forests were similar before harvest and that time since disturbance (and the extent of forest regeneration and maturation) was the primary variable affecting pond characteristics. This assumption may be erroneous, causing problems in interpretation of successional trends from chronosequences (Jackson et al. 1988). Moreover, our chronosequence lacked equal distribution of stands across the 100-year age range; specifically we had only three ponds in the 20- to 60-year age classes. While this reflects an actual lack of aspen stands in this age range in northern Minnesota (Leatherberry et al. 1995), it can make interpretation of age-related trends difficult. Despite these caveats, we felt justified in using a chronosequence for our exploratory study because so little is known currently about the interaction between seasonal ponds and upland forests.

METHODS

Study Area and Pond Selection

We conducted our study on the Chippewa National Forest in north central Minnesota, within the Sucker Lakes watershed. Upland forests of the watershed include mixtures of jack pine (*Pinus banksiana* Lam.), red pine (*P. resinosa* Ait.), and white pine (*P. strobus* L.) on glacial outwash and several types of northern hardwood systems on ground moraine. Forest ecosystems of the watershed are mapped, as part of the National Forest's ecological classification and inventory, and stand ages are known. National Forest personnel have identified all seasonal wetlands in the watershed from 1:24,000 leaf-off color infrared air photography.

We worked within two sugar maple (*Acer saccharum* Marsh.)-basswood (*Tilia americana* L.) ecosystems, specifically ecological landtypes 45 and 46 of the National Forest's classification system (Chippewa National Forest 1996). We selected ponds for study based on the following criteria: i) the surrounding forests fell within one of four broad age classes, 0–14 years since harvest, 15–49 years, 50–75 years, >75 years; ii) ponds and the surrounding forests showed no evidence of recent disturbance since the most recent harvest; iii) pond area was at least 0.02 ha, but less than 0.5 ha; iv) ponds had muck and mineral soil substrates, as opposed to peat; and v) at the time of selection in spring 1997, water depth in the basins was at least 15 cm. Within each stand-age class, we selected four or five ponds randomly from the population of all ponds in the age class in the watershed. We visited each pond to assess the selection criteria, rejecting a pond if necessary and selecting another randomly. In total, we selected 19 ponds for the study. The surface area of the selected ponds ranged from 200 to 2000 m^2 in size. Post harvest ages of the adjacent upland stands ranged from 7 to 101 years.

Field and Laboratory Procedures

Abiotic Variables. We measured hydroperiods and water depths using a metal staff gage placed in the deepest part of the basin of each pond. We placed the gages in the ponds in spring of 1997, immediately after selection. We read the gages weekly to bi-weekly, within a single day for each cycle, during the ice-free season (April 1 through October 31) in 1997–1999. We used only 1998 and 1999 data in this study because many ponds were initially selected late in the spring of 1997; hence, we often missed early hydroperiod data for that year.

When we read staff gages, we also collected water samples if the ponds held water at the time of the reading. We stored samples in 0.5-liter polyethylene bottles under refrigeration at 4° C for a maximum of 30 days before analysis for water chemistry. From these unfiltered samples, we measured solution pH by glass electrode and conductivity using a Yellow Springs Instruments model 35 conductance meter. We determined alkalinity by auto-titration to pH 4.5 (Metler DL20 titrator) followed by Gran plot analysis. Calcium (detection limit = 0.022 mg/L), magnesium (0.009 mg/L), potassium (0.006 mg/L), and sodium (0.003 mg/L) were determined by flame atomic absorption spectrometry (Perkin-Elmer 5000 spectrophotometer). Chloride (0.1 mg/L), sulfate (0.14 mg/L), and dissolved inorganic phosphorus (0.05 mg/L) analyses were done by ion chromatography (Dionex DX 500). We determined nitrate-N (0.02 mg/L), ammonium-N (0.02 mg/L), and total P (0.5 mg/L) by colorimetric procedures on a Lachet Quik Cem 8000 flow injection system, with in-line persulfate digestion for total P. Finally, we measured total organic C using a Dorhmann DC-190 carbon analyzer.

Biotic Variables. In each pond, we established a line transect in 1998 that spanned the long axis of the basin. We recorded cover of sedges, grasses, and coarse woody debris along the transects by line intercept (Brower and Zar 1984). We defined coarse woody debris as trunks and branches greater than 5-cm diameter at their narrowest point within the pond basin. We centered a one-meter-wide belt transect on the line transect and recorded the number of shrub stems (>1 m tall and <2.5 cm diameter at 1.4 m height) rooted in the belt. We determined canopy openness over each pond using a spherical densiometer. Two or three densiometer readings, depending on basin size, were taken in mid-summer along points on the line transect and averaged for each pond. We took readings at a level above the shrub layer (~1.5 m) if one was present. Because of the small size of the ponds, the densiometer readings reflected canopy cover over the basins but, more importantly, integrated canopy openness of the upland forest adjacent to the ponds.

We placed one or two litter traps, depending on pond size, in each basin in 1998 to collect overhead input of coarse particulate organic matter (CPOM). Litter was collected monthly from May through early September and then bi-weekly until early November, with a final collection in early spring 1999. We dried litter at 65° C for 48 hours and then weighed it to determine dry mass.

We sampled macroinvertebrate communities in the ponds during both 1998 and 1999. Each year, we collected samples in late May to collect the spring fauna and again in late June to collect later colonizers. We used a D-frame net sampler (1-mm mesh) because most researchers consider it the optimal device to gather data on macroinvertebrate community compositions from wetlands (Cheal et al. 1996, Batzer et al. 2001). We used three 1-m-long sweeps of the net in each pond. To collect a representative overall sample, one of the sweeps was collected near the pond edge, a second in the pond center, and a third either at a halfway point or in a sub-habitat that otherwise had not been adequately sampled in the previous two sweeps (e.g., emergent plant stands, woody debris). We scraped the net horizontally along the pond bottom to collect both benthic and free-swimming organisms. We pooled the contents of the three sweeps into single composite samples for each pond and preserved the material and invertebrates with 95% ethanol. In the laboratory, we separated invertebrates by hand from mud and detritus and classified them to family or genus. We identified invertebrates using keys from Pennak (1989), Thorp and Covich (1991), and Merritt and Cummins (1996). In particular, we focused on several invertebrates that wetland specialists (see Rader et al. 2001) consider environmentally sensitive, including: fairy shrimp (Anostraca), tadpole shrimp (Notostraca), clam shrimp (Conchostraca), seed shrimp (Ostracoda), water fleas (Cladoceras), dragonfly nymphs (Libellulidae and Aeshnidae), damselfly nymphs (Lestidae and Coenagrionidae), and caddisflies (Limnephilidae, Leptoceridae, and Polycentropodidae).

We used three techniques to survey amphibians, since no technique is adequate for all species or life stages (Heyer et al. 1994). These included calling surveys for breeding anurans, and dip netting and funnel trap collections for amphibian larvae. We conducted calling surveys from April 12 to 15 and from May 17 to 19 in 1998 and 1999. We visited each pond near or after dark and, after several minutes of acclimation, recorded the presence of all species of anurans calling during a 3-minute period. We used D-frame dip nets to sample larvae during late May to early June in 1998 and 1999. Larvae are readily identifiable to species by this point in the season. For each pond, we used a time-constrained search protocol in which two people swept the water for 15 minutes. We held captured amphibians in buckets until the end of the sampling period. After sampling, we identified individuals to species before release. Finally, we used hardware-cloth funnel traps to sample larvae from June 3 to 18. We used two, four, or six unbaited traps in each pond, depending on pond size. Traps were spaced evenly around the pond, perpendicular to the shore, in water deep enough to submerge most of the trap yet still have an air pocket for amphibians to breathe. In 1998, half of the traps in each pond had 6-mm mesh, while the remainder had 3-mm mesh. After 1998 trapping, we determined that the smaller mesh size was more efficient in capturing smaller sized larvae (R. Buech,

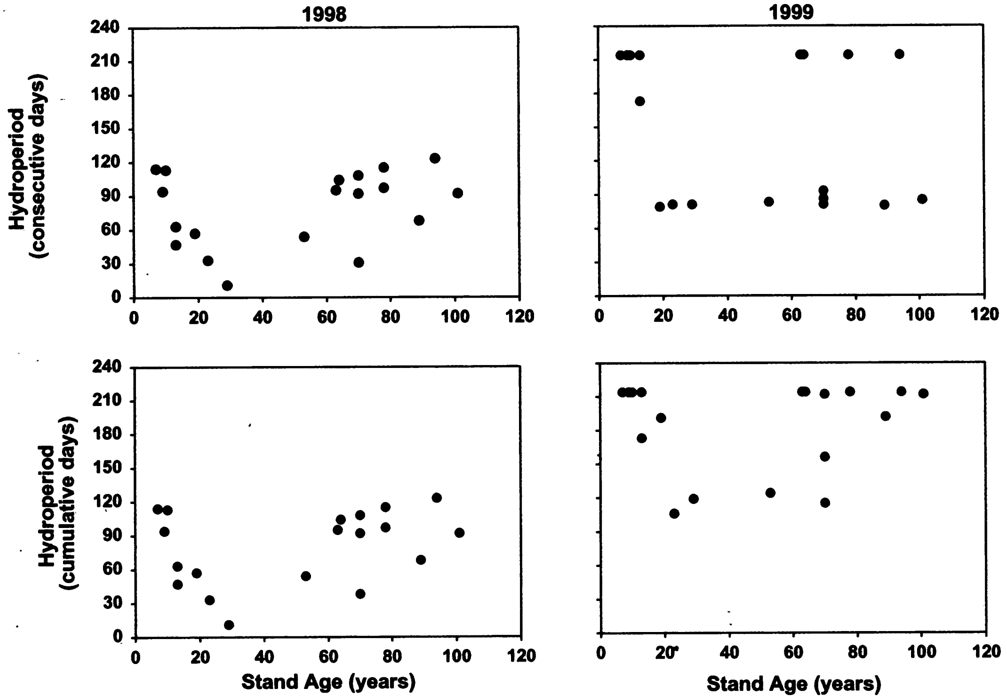

Figure 1. Hydroperiods as a function of adjacent forest age in 19 seasonal ponds in 1998 and 1999. In each year, the top frame is consecutive days with water between April 1 and October 31, while the bottom frame is cumulative days with water during the same period.

personal observation), thus all traps had 3-mm mesh in 1999. Traps were set out on Mondays, checked daily on the following three days, and removed. On each of the check days, we identified the trapped amphibians to species before release.

Data Analyses

We summarized and analyzed hydroperiods in each of the two sample years (1998–1999) in two ways, including consecutive days with water (from April 1 to October 31) and cumulative days with water (from April 1 to October 31). Values for the water chemistry variables are the mean of two sample years (1998–99). For each pond in each year, we selected a single sample date in mid- to late-spring that was midway between snow melt in early spring and significant dry down by mid-summer. Our goal was to characterize water chemistry during conditions that avoided significant dilution from recent snow melt and concentration as the ponds dried.

We analyzed aquatic invertebrates separately by year (1998 and 1999). For these analyses, we first compared overall abundances and numbers of families among ponds. Next, we considered only sensitive taxa. Finally, we examined numbers of dominant families (i.e., those that were collected from at least two-thirds of the ponds).

We summarized amphibian data in several ways, including abundance, species richness, and species presence or absence. We used calling surveys to determine breeding anuran presence or absence in each pond. We summarized larval abundance in each pond by species, separately for 1998 and 1999, using both dip-net counts and capture rate from funnel traps. Dip-net data are expressed as larvae per 15-minute sweep. Funnel-trap capture rate is the number of larvae caught * trap^{-1} * night^{-1}, averaged over all traps and nights. We based our species richness determination on occurrence as determined by the combination of all survey methods.

We analyzed most variables by regressing them on stand age (1998 stand age) using linear models. We fit an exponential (rise to a maximum) model to the CPOM flux data because research in similar forest types showed that annual foliar production follows this pattern with time after disturbance (Jurik et al. 1988). Where data were heteroskedastic (canopy openness, amphibian species richness, and invertebrate abundance measures), raw numbers were log-transformed (x or x+1), as recommended by Allan (1984), and analyses run on the transformed data. Examination of residual plots indicated that regression assumptions were met. We analyzed occurrence of breeding anurans using logistic regression. Because of the large number of regression analyses run (48), we used a minimum alpha level of 0.025 to assess significance of a relationship.

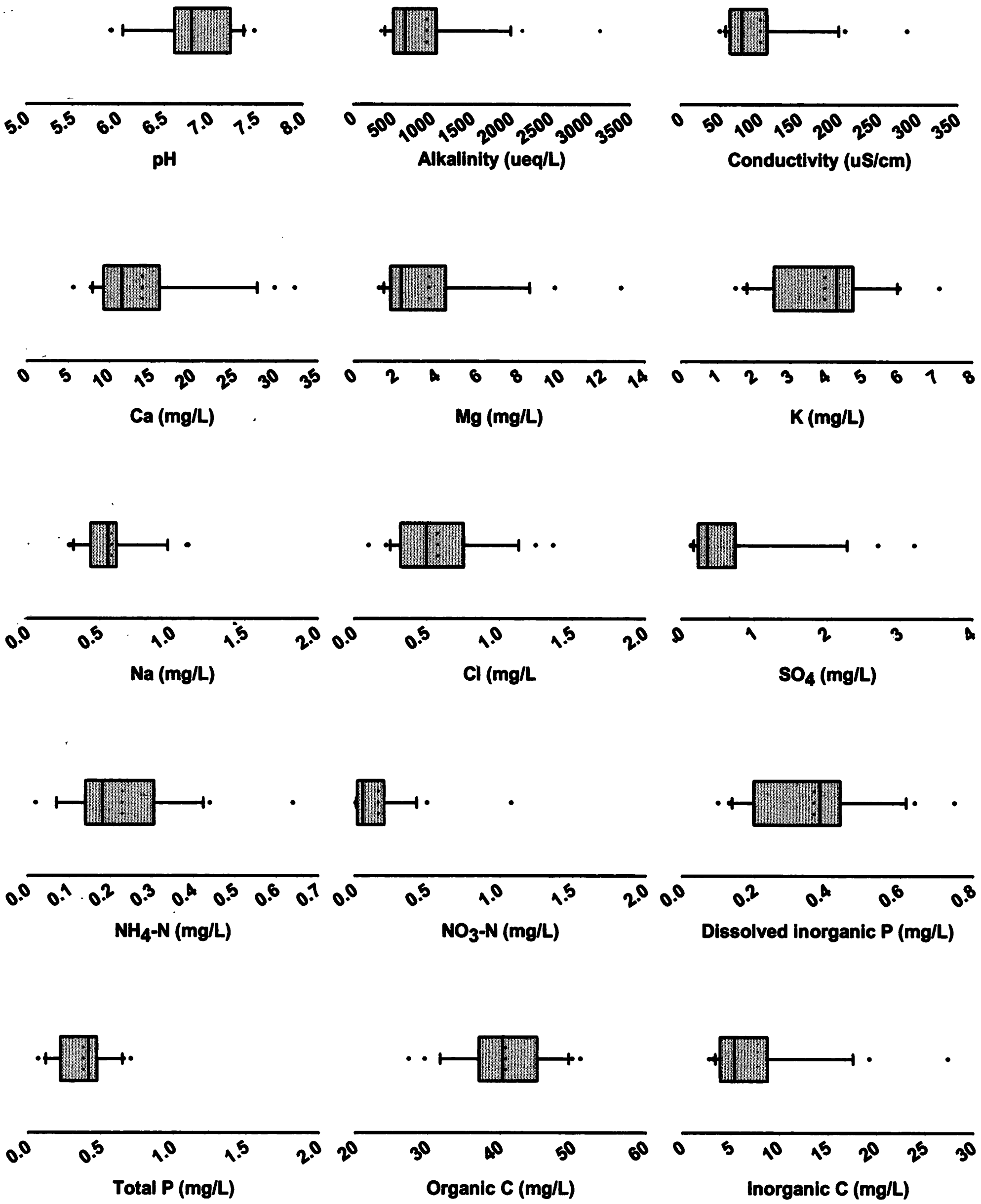

Figure 2. Water chemistry characteristics for 19 seasonal ponds. Each box plot shows the mean (dotted vertical line), the median (solid vertical line), the 10th, 25th, 75th, and 90th percentiles, and outliers beyond the 10th and 90th percentiles. Values are the mean of 1998 and 1999 samples.

RESULTS

Hydrology

Water was present for some length of time in all ponds in both years. However, hydroperiods were much shorter in 1998 than in 1999 (Figure 1). In 1998, three ponds were dry within 35 days of being ice-free, while the longest hydroperiods were about 120 days, compared to 220 days in 1999 (Figure 1). Neither consecutive nor cumulative days with water were significantly related to stand age in 1998 or 1999 (Figure 1). However, in both years, hydroperiods seem to be shorter for ponds in the middle stand ages (20–60 years) than in both younger and older stands. Unfortunately, poor representation of ponds in this portion of the chronosequence makes interpretation difficult. Maximum water depths ranged from 0.41 to 1.47 m in 1998 and 0.81 to 1.79 m in 1999 but were unrelated to stand age in either year (data not shown).

Water Chemistry

Most water chemistry variables were highly variable among ponds (Figure 2) but were similar across years

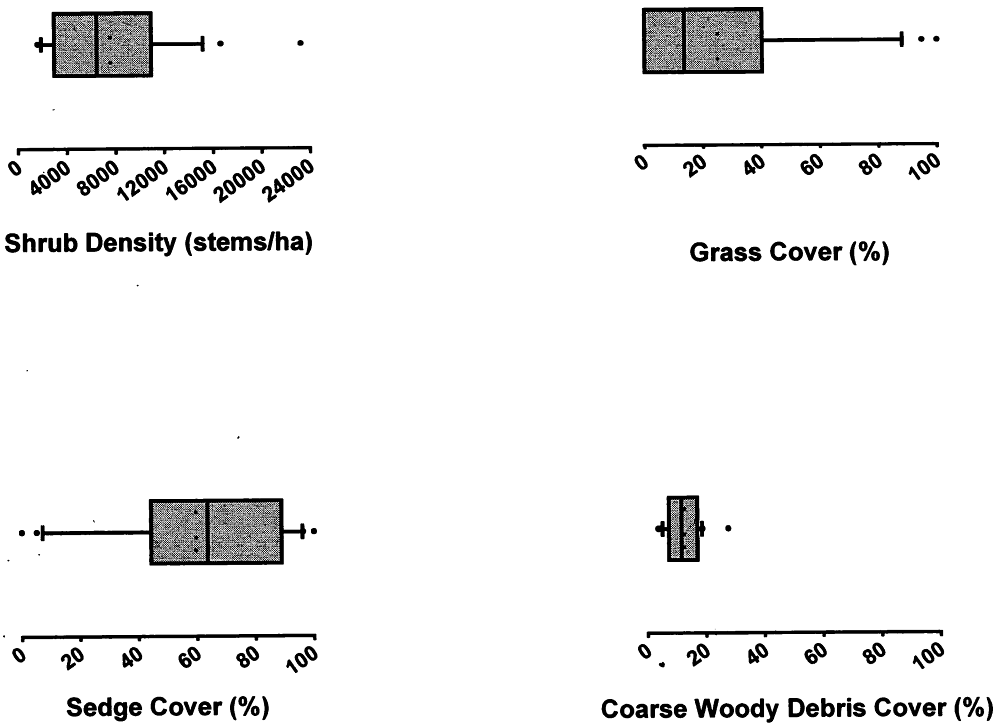

Figure 3. Shrub density (stems/ha), grass cover (%), sedge cover (%), and coarse woody debris cover (%) in 19 seasonal ponds in 1998. Each box plot shows the mean (dotted vertical line), the median (solid vertical line), the 10th, 25th, 75th, and 90th percentiles, and outliers beyond the 10th and 90th percentiles.

within ponds. Thus, the numbers used to calculate the figure are the means of 1998 and 1999 samples. Conductivity values suggest that most ponds derived their water from surface runoff (<100 μS/cm), but a few were likely fed by a mixture of surface and ground waters. None of the water chemistry variables were significantly related to stand age (data not shown).

Vegetation Characteristics

With the exception of coarse woody debris, vegetation cover variables (measured in 1998 only) were highly variable among ponds (Figure 3). However, none of these variables showed any significant trends related to stand age (data not shown).

Mean canopy openness above the pond basins decreased predictably (adj. $R^2 = 0.23$, $p = 0.023$) with stand age (Figure 4a). The canopy above the youngest stands was about 70% open. Openness decreased to about 10% in the oldest stands. The relationship was stronger with exclusion of two outlier ponds (open circles in Figure 4a; $R^2 = 0.62$, $p = 0.0002$). The relationship between stand age and canopy openness may be non-linear, with a rapid decrease in openness early in stand development and steady levels thereafter. However, we had too few ponds in the middle age-range to assess this trend with any certainty.

Coarse particulate organic matter (CPOM) flux into the ponds increased with stand age (Figure 4b). Litter inputs averaged about 40 $g*m^{-2}*yr^{-1}$ in the youngest stands, increasing exponentially and predictably (adj. $R^2 = 0.79$, $p < 0.0001$) with stand age to about 300 $g*m^{-2}*yr^{-1}$ in the oldest stands.

Macroinvertebrates

Water was present in 15 of the ponds during late May 1998 but in only 12 ponds during June. Because it was wetter in 1999, we were able to collect invertebrates samples from 18 ponds during late May and 15 ponds during June. In both years, the ponds that dried early were those occurring within 20- to 60-year-old forests (Figure 1). Overall, 44 families of aquatic macroinvertebrates were collected from the ponds, and most of these families contained multiple genera. However, only 14 families were common and widespread (i.e., occurred in at least 66% of the ponds). Mollusks were particularly abundant. Fingernail clams (Bivalvia:Pisididae = Sphaeriidae) occurred in every pond and numerically dominated collections during both years. Snails (Gastropoda: Physidae, Lymnaeidae, and/or Planorbidae) were also abundant in most ponds. Among insects, fly larvae (Diptera: Chironomidae and Chaoboridae) and beetle larvae and adults (Coleoptera: Dytiscidae and Hydrophilidae) were widespread in both years, although only the chironomid midges ap-

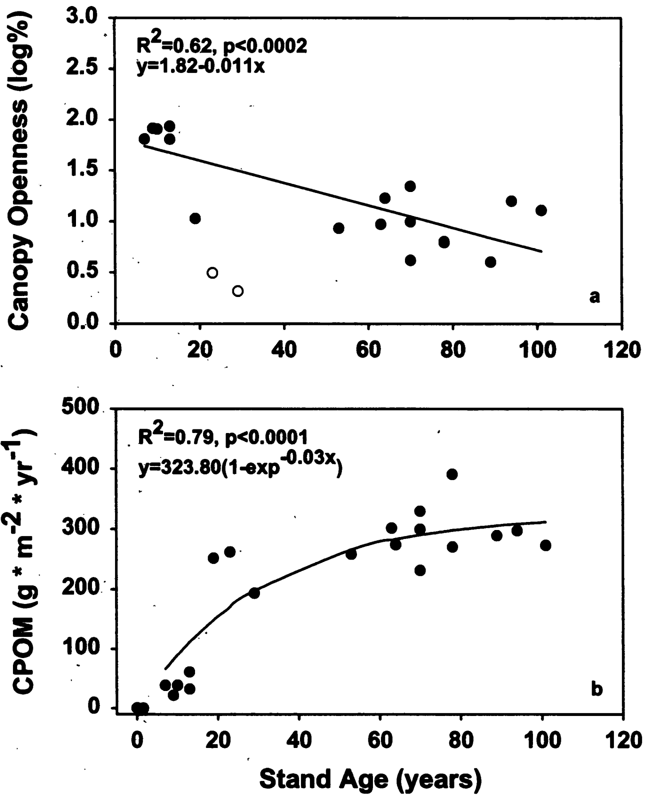

Figure 4. Canopy openness (a) and coarse particulate organic matter flux (CPOM) (b) as a function of adjacent forest age in 19 seasonal ponds. Regression results in 4b exclude the two outliers (open circles).

proached the mollusks in abundance. In 1998, but not 1999, Libellulidae dragonfly nymphs, Haliplidae beetle larvae and adults, and Limnephilidae caddisfly larvae were widespread and in some places abundant. Aquatic worms (Oligochaeta: Tubificidae) and leeches (Hirudinea: Glossophoniidae) were widespread in 1998, but only the former were common in 1999. Although numerous crustacean families occurred in the ponds, only cladoceran water fleas (Brachiopoda: Daphnidae) were widespread (both years).

Total macroinvertebrate numbers varied by an order of magnitude among ponds (138 to 1452 invertebrates/pond sample), but little variation was explained by stand age (data not shown). Moreover, family richness was similar across the age gradient in both years (data not shown).

The eight indicator taxa (fairy, tadpole, clam, and seed shrimp, water fleas, dragonfly nymphs, damselfly nymphs, and caddisflies) were rare in most ponds. Richness of these taxa did not vary significantly with stand age; although in 1999, somewhat greater numbers of sensitive groups were collected from the most recently harvested sites than from those in older stands. Population sizes of macroinvertebrate families were unrelated to stand age in both years (data not shown).

Amphibians

We conducted calling surveys for breeding adults at all ponds in both years. However, because of short hydroperiods in 1998, particularly for ponds located in 20- to 60-year-old forests, we were able to dip-net in only 12 ponds and trap in only 10 ponds. We were able to net and trap in all 19 ponds in 1999.

We recorded five species of amphibians in both 1998 and 1999, including wood frogs (*Rana sylvatica* Baird), spring peepers (*Pseudacris crucifer* Wied.), blue-spotted salamanders (*Ambystoma laterale* Green), western chorus frogs (*Pseudacris triseriata* Wied.), and gray treefrogs (*Hyla versicolor* Le Conte). Stand age was not a significant predictor by logistic regression for presence of calling anurans in either year (1999 data shown in Figure 5a-d). Rates of larvae capture by both dip netting and trapping varied widely among ponds and years. Most ponds contained wood frog larvae in 1999. However, wood frog larvae in 1998 and larvae of the other four species in both years were rare, occurring in five or fewer ponds (data not shown). For wood frogs in 1999, we found no significant relationships between stand age and larval abundance (for either dip-net or trap data) (Figure 5e-f). Similarly, considering all species together, richness did not vary predictably with stand age in either year (data not shown).

Biotic Responses to Canopy Openness and CPOM Flux

Vegetation cover variables (sedge, grass, coarse woody debris, shrub density) were unrelated statistically to canopy openness (data not shown). However, sedge cover was always high (>80%) in ponds with open canopies (>60%) but highly variable (0–100%) when canopy openness was low (<25%). Conversely, shrub densities were always low (<6000 stems/ha) when canopy openness was high (>60%), but densities were highly variable (0–25,000 stems/ha) when canopy openness was low (<25%).

Four macroinvertebrate variables (of 18 variable * year combinations examined) were related linearly to canopy openness, including total marcroinvertebrate abundance in 1998, sensitive taxa richness in 1999, Physidae snail abundances in 1998, and Haliplidae beetle abundance in 1998 (Figure 6). For all of these variables, values increased linearly with increasing canopy openness, although a lack of ponds in the mid-range of canopy openness makes definitive interpretation of linear trends problematic. None of the ma-

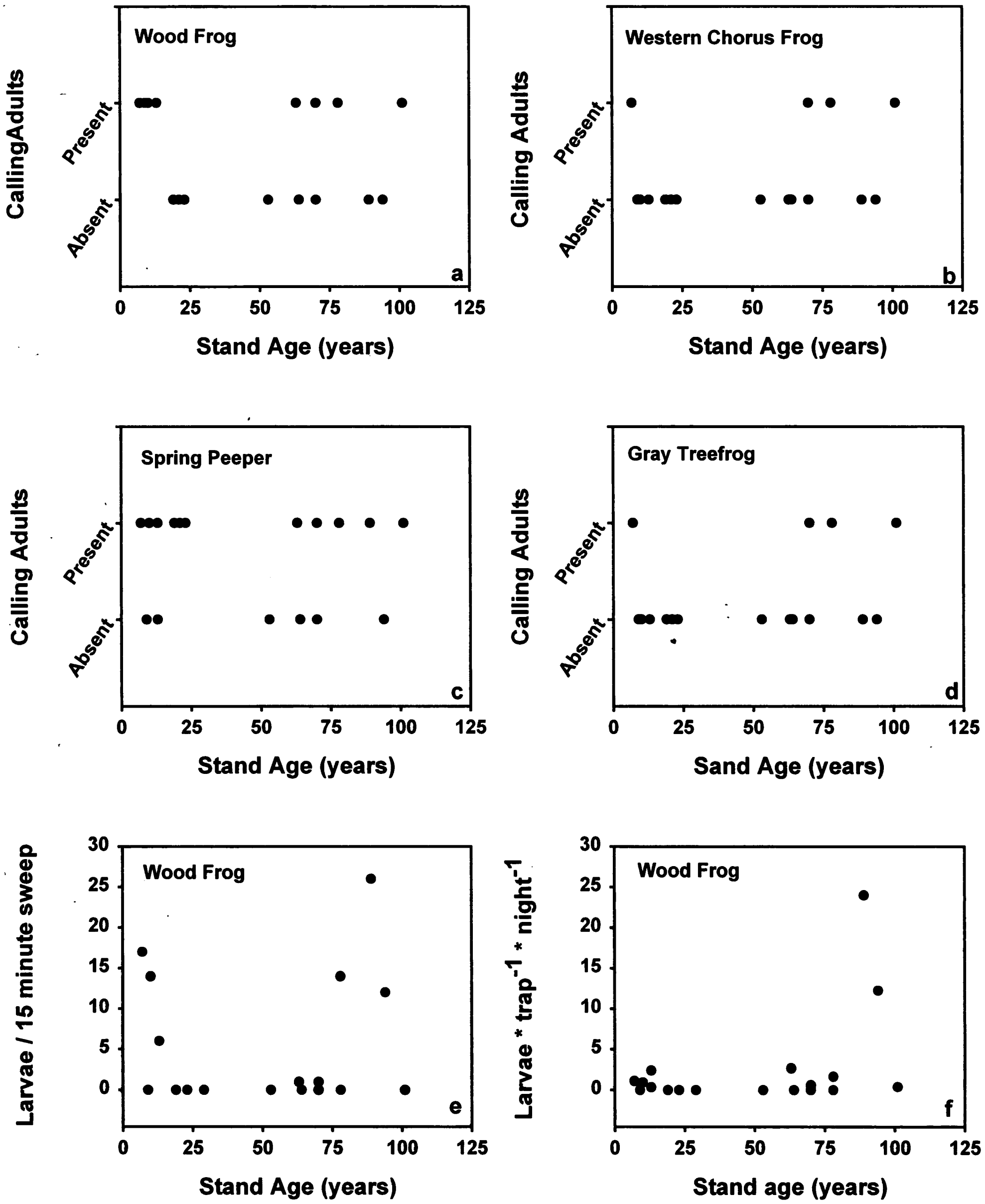

Figure 5. Occurrence of calling anurans as a function of adjacent forest age in 19 seasonal ponds (a-d) in 1998 (1999 results were similar) and abundance of wood frog larvae by two sample methods in 1999 (e-f).

croinvertebrate variables were clearly related to CPOM flux (data not shown).

There were weak (although non-significant) relationships between presence of calling wood frogs and canopy openness and CPOM flux (Figure 7). Specifically, wood frogs were always present in ponds with high canopy openness (>60%) and low CPOM flux (<100 g * m^{-2} * yr^{-1}). Occurrences of the other calling anurans were unrelated to these variables (data not shown). There were no consistent relationships between canopy openness or CPOM flux and larval abundance (from either dip-net and trap data) or species richness of amphibians (data not shown).

DISCUSSION

We discovered little compelling evidence that age of the adjacent upland forest affects abiotic and biotic variables of seasonal ponds, including hydroperiod, water chemistry, water depth, overall macroinvertebrate abundance and diversity, macroinvertebrate population sizes, calling of breeding anurans, or abundance of amphibian larvae. The only significantly responses to stand age were for canopy cover and CPOM flux. A potential reason for these findings is that our youngest stand was already seven years old at the time of sampling. Thus, we may have missed immediate post-

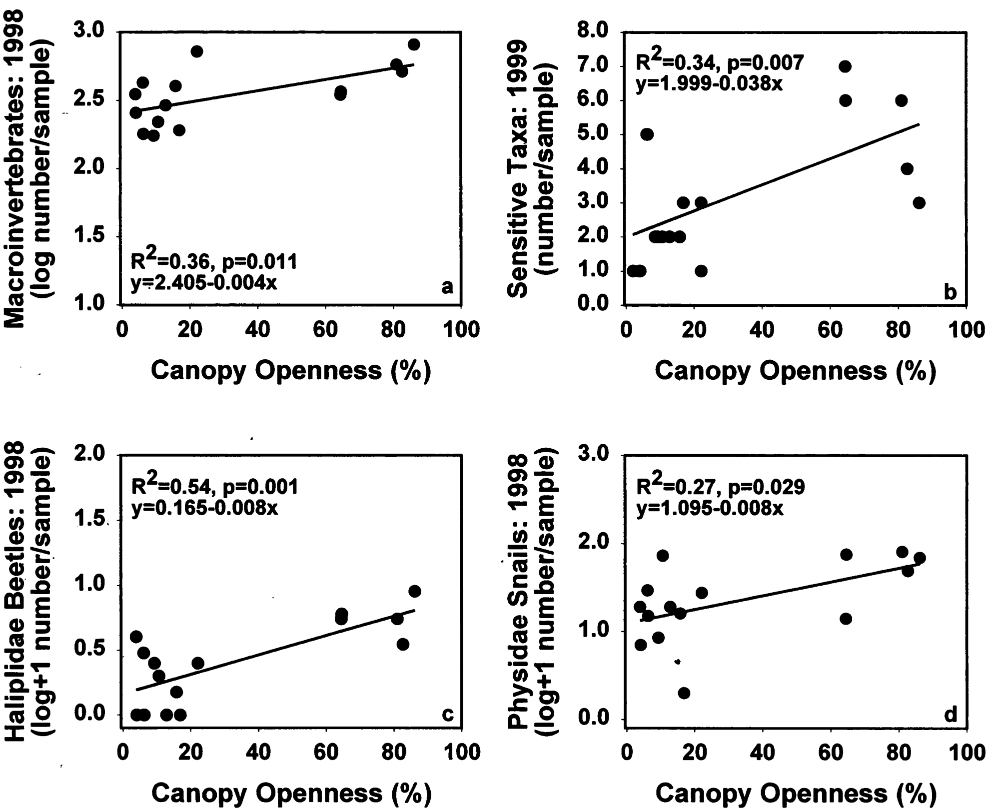

Figure 6. (a) Total macroinvertebrate abundance in 1998, (b) sensitive taxon richness in 1999, (c) Haliplidae beetle abundance in 1998, and (d) Physidae snail abundance in 1998 as a function of canopy openness in 15–18 seasonal ponds (see text for a list of sensitive taxa).

harvest responses for many variables. Results from Batzer et al. (2000), from a study of ponds in southern pine plantations, support this idea. Temporal patterns for many of the pond characteristic they measured, including several of those measured in the current study, suggest that changes initiated by harvest of the adjacent forest persist for only 15 to 20 years.

We interpret our results cautiously because of the inherent problems of using space-for-time substitutions in studies of successional trends (Jackson et al. 1988). As with any chronosequence, we cannot be certain that time since upland forest disturbance is the only important variable influencing our study ponds. Consequently, the lack of age-related trends for most variables could result from differences among ponds in other driving factors. Moreover, poor representation of ponds in 25- to 60-year-old stands may obscure important age-related trends. For instance, our data suggest that hydroperiod is longest in the youngest (<15 years) and oldest (60 years) stands, particularly in 1998 (Figure 1a), but we have too few ponds in the middle age range to assess this potential curvilinear relationship.

While pond water chemistry was unrelated to forest age, mean and maximum values for some parameters, especially those derived principally from organic matter (e.g., NH_4-N, phosphorus), are much higher than reported for most natural waters (e.g., Wetzel 1983, Holmes et al. 1999). However, the values are similar to those reported for somewhat larger shallow water wetlands in the region (Verry 1983, 1985). In these wetlands, and we suspect in our seasonal ponds, hypereutrophic conditions can develop over time as water levels decrease, leading to high concentrations for some solutes (Verry 1983).

While interest is growing in understanding impacts to wetlands from forest harvest (Richardson 1994, Richardson and McCarthy 1994, Prenger and Crisman 2001), until recently, ecologists have largely ignored impacts to small seasonal ponds (Batzer et al. 2000). Our primary objective for this study was to relate changes in pond characteristics over time to differences in adjacent upland forest age following harvest. However, stand age is only a surrogate measure for developmental changes occurring in forest stands after harvest, since it says nothing about the actual mechanisms that may influence pond biota.

In our study, changes in canopy openness, which correlated with stand age, explained variation in several macroinvertebrate characteristics. We found re-

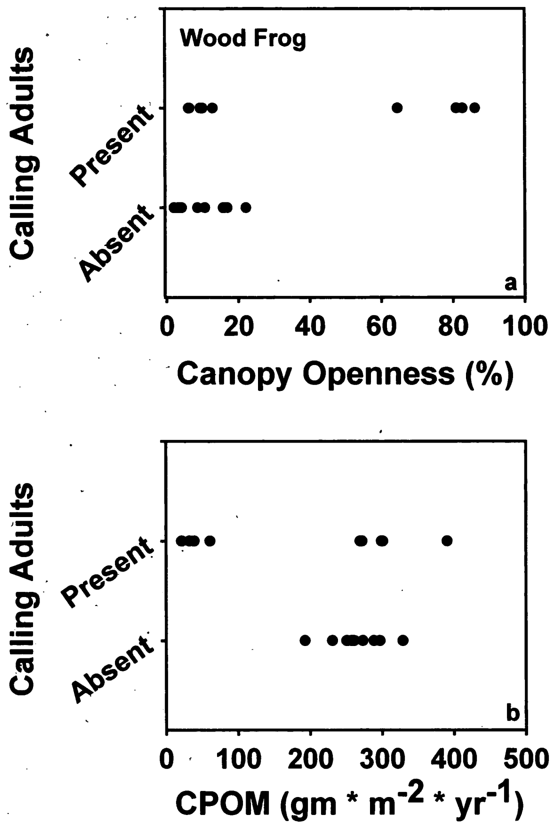

Figure 7. Occurrence of calling wood frogs in 1998 as a function of canopy openness (a) and CPOM flux (b) in 19 seasonal ponds.

sponsive taxa to be largely algivores (e.g., Physidae snails, Haliplidae beetles). In streams, increased sunlight and nutrient input after riparian harvest often result in increased algal growth and increased numbers of algivorous invertebrates (Hawkins et al. 1982, Noel et al. 1986, Stone and Wallace 1998). The response by pond algivores to canopy openness in our study suggests that a similar ecological mechanism is important (Prenger and Crisman, 2001). These populations then decrease as the canopy closes during stand development.

Our amphibian calling data, and work by others (Werner and Glennemeier 1999), suggest that wood frogs breed in both closed- and open-canopy ponds. However, our data also suggest that they may prefer an open-canopy condition, since calling adults were always present in these ponds but sometimes absent in closed-canopy ponds. Perhaps early spring air and water temperatures generally are favorable for breeding in open-canopy ponds, whereas environmental conditions are more variable in closed-canopy ponds.

CPOM flux was highly correlated with stand age, but it was unrelated to macroinvertebrate variables, perhaps because shredders were largely absent from our study ponds. Wood frogs were always present in ponds with low CPOM flux. However, in the absence of a plausible mechanistic explanation for this pattern, we suggest that it simply reflects the correlation between canopy openness and annual leaf litter production and flux into the ponds.

CONCLUSIONS

We found only limited evidence that changes in adjacent upland forest age after harvest alter biophysical characteristics of seasonal ponds. Responsive variables did include canopy closure and CPOM flux. Canopy openness may be linked mechanistically to pond biota through effects on air and water temperatures and light availability. In fact, we did find that several macroinvertebrate variables changed predictably with canopy openness. The responses we detected reflect changes in stand characteristics during forest development after disturbance, rather than impacts from harvesting *per se.* As such, one might expect and be able to predict recovery of pond characteristics as the new forest develops. We suggest this cautiously because of the problems inherent in studies using space-for-time substitutions to make prediction about temporal trends. To address this concern, we recently initiated a controlled experiment that examines responses in pond characteristics to various harvesting treatments in the adjacent forest, including clearcutting to the pond edge and various sizes of buffers around the pond.

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